

LEARNING IN THE SPINY LOBSTER *PANULIRUS ARGUS*

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Although Bethe (1898) believed crustaceans in general could not learn by experience, subsequent research by many investigators has proved that cladocerans, isopods, crayfishes, hermit crabs and several kinds of brachyuran crabs can variously show habituation, discrimination learning and trial-and-error learning (reviews: Warden, Jenkins and Warner, 1940; Thorpe, 1956; Schöne, 1961; recent research paper: Datta, Milstein and Bitterman, 1960). In these different cases visual, chemoreceptor, kinesthetic or tactile elements were involved in the afferent components of the behavior patterns studied. As is typical for learning, these data (plotted as error scores) usually fall on curves resembling exponential decay functions with a large initial number of errors which, with training, are rapidly reduced at first and then later decrease more and more slowly (Hull, 1952; Hilgard, 1956; Bush and Estes, 1959).

In attempting to demonstrate polarized light vision in decapod crustaceans, training experiments were undertaken with *Panulirus* to determine whether different planes of polarization could be learned as cues for the solution of a two-choice spatial problem. While the lobsters failed to use the polarization pattern in this way, they were able to make their spatial choice on the basis of brightness discrimination or to learn always to choose the same side for attaining a goal. The present report describes these experiments and briefly considers their comparative behavioral implications.

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METHODS

The experimental animals were juvenile specimens of *Panulirus argus* (Latreille) 8–12 cm. in body length. They were tested in an experimental discrimination box in which they were trained to walk forward (in air) to one of two compartments at the far end (Fig. 1). Each compartment had a large rectangular exit hole in its floor; one was open and led down to the aquarium below in which the lobster was normally kept; the other was closed by a wire screen which prevented

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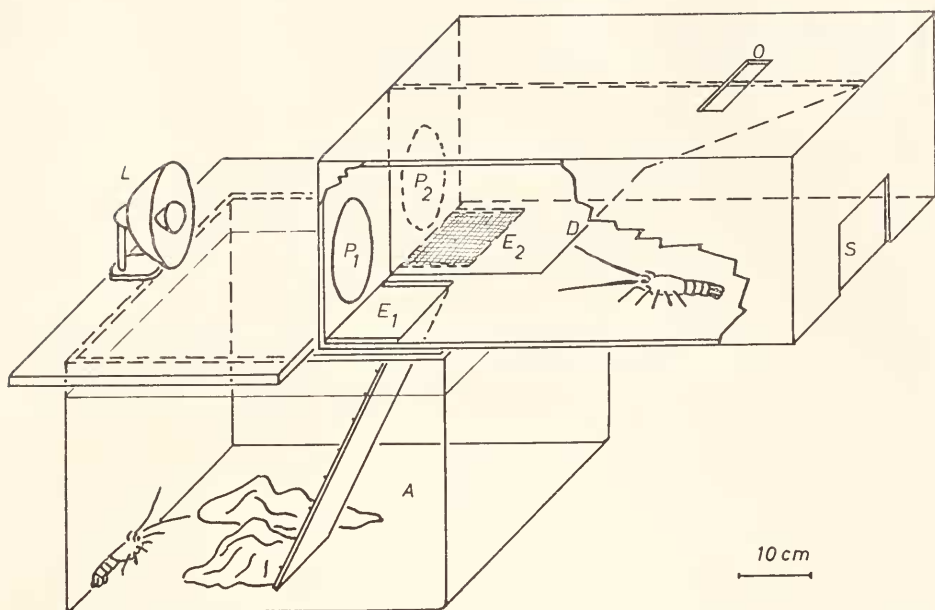


FIGURE 1. Two-choice spatial discrimination box used to train *Panulirus*. *A*, aquarium containing sea water; *D*, partition dividing front of box into two compartments; *E*₁, open exit from one compartment to aquarium below; *E*₂, blocked exit in other compartment; *L*, light source illuminating conditioning stimuli (*P*₁, *P*₂); *O*, slit for observing the lobster's behavior during tests; *P*₁, *P*₂, circular illuminated areas used in experiments training to brightness and those designed to train to plane of polarization; *S*, starting place for runs.

the animal's return home. The lobsters were observed through a peep hole and their course recorded on a floor plan of the box.

Two conditioning stimuli were presented when desired at a circular opening in the far wall of each compartment. These apertures were covered with translucent paper and illuminated from behind. The intensity of these stimuli could be altered by using additional layers of the translucent paper, and polarizers (Polaroid HN38 neutral polarizing filters) could be placed in the light paths to effect nearly 100% linear polarization of the illuminated areas.

Experiments were carried out as follows. The *Panulirus* were tested one at a time by placing them at the entrance of the experimental box facing the two goal compartments which were at the opposite end (Figs. 1 and 2). For animals which walked to the compartment with the open exit hole without entering the closed compartment a score of "correct" was kept; an error was recorded for those which walked into the closed compartment (score of "incorrect") and for those which stopped and remained anywhere in the back part of the box for five minutes ("non-spontaneous runs"), after which the lobsters were prodded into action and led in the correct direction with a small stick. When spontaneous locomotion was particularly circuitous or slow, this stick was also used to prod the lobster into action.

In addition to the error scores (in per cent per three trials) two other kinds of data were taken: (1) percentage of nonspontaneous runs and (2) percentage of runs in which tail-flexing reactions occurred.

In various experiments groups of individuals varying in number from 6 to 11 were given 2 to 6 tests per day, and the observations were repeated for 6 to 22 days. In certain cases the performances of trained and inexperienced individuals were compared.

The three main series of training experiments all followed the general procedure outlined above but differed in certain important details.

1. *Training to brightness.* Ten individual inexperienced lobsters which had never been in the experimental box before were used in these tests. The conditioning stimuli differed in intensity, and the more intense one was always on the side of the compartment with the exit open to the aquarium below (positive side). During the first 9 days I_{pos} was three times as great as I_{neg} ; during the remaining 13 days I_{pos} was five times as great as I_{neg} . The first day each animal was tested three times, for the next 9 days five times per day, and for the last 12 days six times per day (about 119 runs per individual or 1188 altogether). To control against

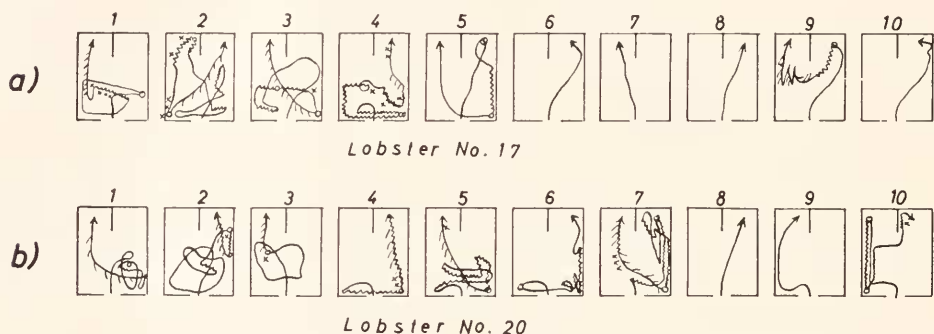


FIGURE 2. First ten runs of (a) a lobster (No. 17) which learned relatively quickly to discriminate brightness in choosing the right course to the open exit, and (b) a lobster (No. 20) which was slow in learning this task. The different parts of the animal's track are marked with the following symbol: full line = running forward; zig-zag line = running backward; small open circle = stop; cross hatching next to line = guiding by a stick; crosses = tail flexing movement.

the lobsters merely learning "side" the positive side was changed alternately from right to left for the first 12 days; then sides were shifted in random order for the next 10 days.

2. *Training to polarized light.* One series of measurements (A) was made on 11 inexperienced lobsters; a second series (B) was run with 10 experienced animals.² For Series A the box's wooden walls were unpainted. For Series B the walls of the experimental box were painted with aluminum paint in order to minimize reflection-refraction artifacts arising from differential effects of the walls on the total light pattern visible to the lobsters. The two conditioning stimuli had the same intensity and degree of linear polarization, but in one (the positive side) the e -vector was horizontal, while in the other it was vertical. Five tests per day per animal were made in each series. The horizontal polarization was regularly alternated from left (l) to right (r) in successive tests of Series B, but there were some irregularities in Series A which ran: rrlrlrlrlrlrlrlrlrlrlrlrlrlrlrl. Series A

² These had previously been used in the experiments on training to brightness.

lasted 6 days (about 30 tests per animal, total 327), Series B, 11 days (55 tests per animal, total 550).

3. *Training to side.* Six inexperienced lobsters were run in the experimental box for 9 days with the left compartment's exit open to the aquarium throughout. The intensities of the two light windows were equal and they were not polarized. Two tests were made per animal on the first day and three during the succeeding 8 days, making 26 per animal (total 156).

RESULTS

A. General behavior

In the present experimental situation *Panulirus*' behavior was made up of activity sequences containing one or more of four locomotor components: (1) no locomotion, (2) forward walking, (3) backward walking, and (4) tail-flexing movements.³ The actual paths followed were, of course, characteristically affected by the amount and rate of turning. Examples of the resulting trails are given as two series of 10 trials each for individual lobsters (Fig. 2).

Evidently these activity sequences differ in three major ways which are inter-related: (1) degree of spontaneity, (2) directness from starting point to end point, (3) particular locomotor components involved. Thus the most direct trails (Fig. 2a, Runs 7 and 8; Fig. 2b, Run 8) were started spontaneously, and consisted only of forward walking, at first straight ahead, then gradually turning towards the side with the open exit.

In slightly less direct paths the animal also started spontaneously and walked forward all the way but it turned more strongly towards the positive side, struck the side wall and followed this for a while until it turned in the opposite direction towards the exit (Fig. 2a, Runs 6 and 10; Fig. 2b, Run 9).

As the paths became less direct than this, more turning, stopping and backward walking appeared (Fig. 2a, Runs 5 and 9; Fig. 2b, Runs 4 and 10). Spontaneity was reduced and tail-flipping escape reflexes were evident. Finally, in the least direct runs the animals often did not leave the back part of the box spontaneously. In such cases they frequently had to be guided to the open exit with the stick. Backward walking, stopping and escape reactions occurred often (Fig. 2a, Runs 1, 2, 3 and 4; Fig. 2b, Runs 2, 5 and 7).

Some of the variation in these behavior patterns of *Panulirus* is due to individual peculiarities since the number and kind of certain loops, turns or backtracks tend to be similar in successive trials for the same lobster but to differ from one animal to another. The correlation of alterations in response with learning and the three types of training employed is considered in detail in the next section.

B. Training experiments

In running the two-choice maze of the present setup the short spontaneous paths over which the animals have walked directly forward to the open exit represent the best behavior if prompt return to sea water in their aquarium is considered the goal.

³ These arise as strong flexions of the abdomen (Lochhead, 1961; Wiersma, 1961) which may result in the animal's projecting itself backward several centimeters in a response often termed an escape reflex.

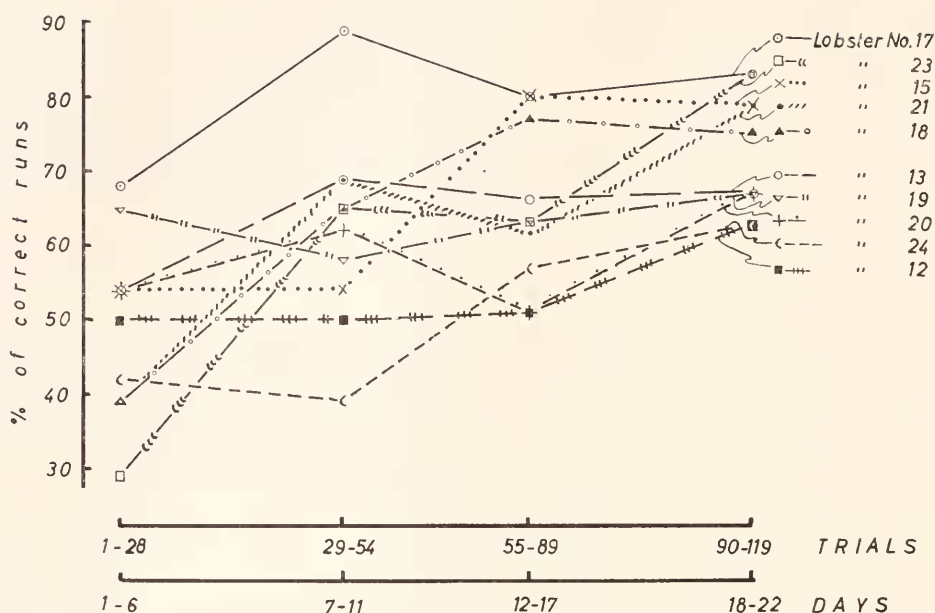


FIGURE 3. Learning curves for 10 individual lobsters training to brightness. Points indicate percentages of runs for the periods in trials (as well as days) specified on the abscissa.

Conversely, meandering runs with stops, walking backward, escape reactions and failure to reach the goal without guidance represent the worst performances. Under appropriate conditions of training and with test animals having a tendency to associate a conditioning stimulus with the goal, the poor responses shown initially by inexperienced animals improve progressively to a better performance level.

However, the amount of improvement and its rate during different parts of the training period were quite different in individual animals (Fig. 3). The factors involved in such variations remain largely unstudied. Nevertheless in certain experiments poor or insignificant improvement can be attributed to the development of certain preferences largely unaffected by the kind of associations tested. Thus in Series B of the training to polarized light, 5 of the 10 animals tested preferred one side of the box regardless of changes in the side of the open exit. This habit may be so rigid as to persist even when the positive side was never made the one preferred.

An example of this type of behavior, quite resistant to conditioning in the present setup, is shown in Figure 4. Here the alternation of positive side (a, 1; b, 1) from left to right was succeeded by the open exit being maintained only on the left (a, 2; b, 2). Despite this, Animal 12 continued to turn right, and even after a few correct responses, returned to its persistent incorrect right turn. Animal 15 showed a comparable predominance of right-hand turns for the greater part of the series but toward the end seemed to learn the left turn required to reach the positive side.

A summary of the numbers and types of runs made in each of the three kinds of training experiments is presented in Table I.

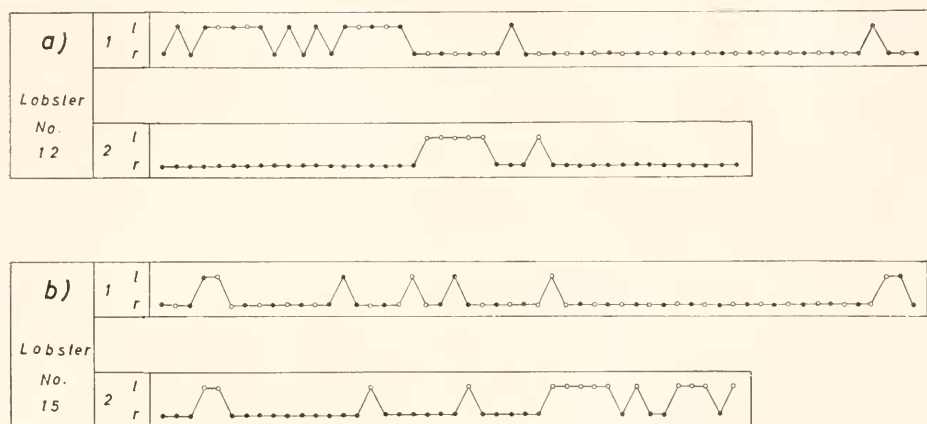


FIGURE 4. Serial representation of training runs of two experienced lobsters to polarized light (sequence from left to right). In series a1, b1 the open exit (positive side) was alternated regularly; in series a2, b2 the positive side was always to the left. Correct runs are represented by open circles, incorrect runs by filled circles. Development of a tendency to run towards the right side is shown by lobster No. 12 which kept this tendency even when the positive side remained left; lobster No. 15 did not, having finally changed to the positive side.

1. *Training to brightness.* Initially the average error score of the 10 animals tested was 93%. This had fallen to 35–40% after 30–40 trials and continued to diminish (but at a reduced rate) to about 20% by the end of the experiment (119 trials) (Fig. 5, error curve). The fraction of nonspontaneous runs was also high during the first trials (57%) but fell to about 10% after 10 trials and became zero for the last 40 trials (Fig. 5, curve of nonspontaneous runs). Similarly, the percentage of runs showing tail-flexing movement was maximum in the first trials (30%), declined irregularly during the next 30 trials and settled down to 0–7% in

TABLE I
Occurrence of tail-flexing movements during different kinds of runs in four series of training experiments

Runs	Training to brightness			Training to polarized light						Training to side		
				Series A			Series B					
	Total	With tail flexes		Total	With tail flexes		Total	With tail flexes		Total	With tail flexes	
No.		%	No.		%	No.		%	No.		%	
Correct	745	6	1	157	5	3	251	23	9	88	0	0
Incorrect*	394	82	21	156	66	42	271	86	32	33	5	16
Nonspontaneous	49	15	31	14	12	86	28	13	46	35	10	29
Total	1188	103	9	327	83	26	550	122	22	156	15	10

* Incorrect runs = error runs minus nonspontaneous runs.



FIGURE 5. Mean learning curve for 10 lobsters training to brightness. Points represent percentages of the runs in three trials.

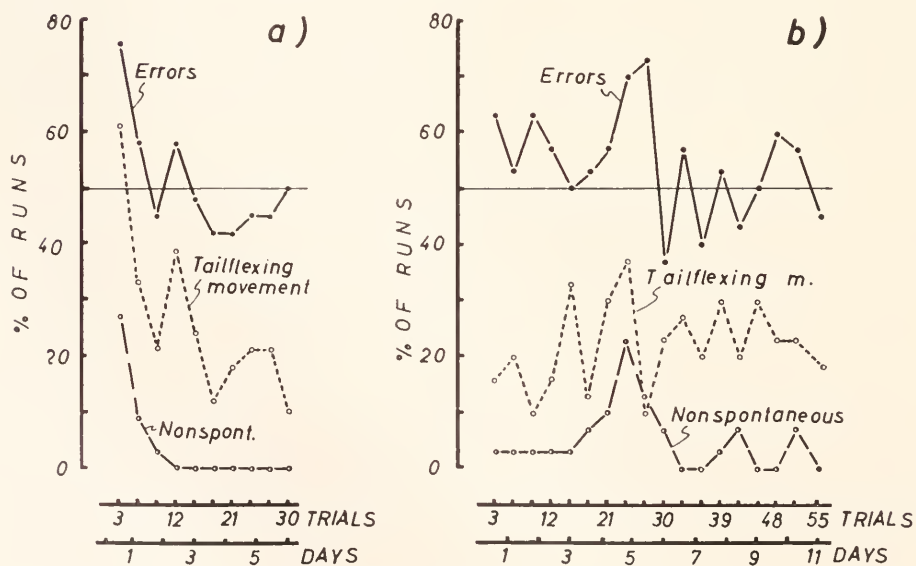


FIGURE 6. Mean learning curves for lobsters where training was attempted to plane of polarization. (a) Series A, 11 previously untrained animals, (b) Series B, 10 previously trained animals. Points represent percentages of the runs in three trials.

the last 30 trials (Fig. 5, curve of tail-flexing movement). The error curve and curve of tail-flexing movements at least show signs of flattening out, or even of a temporary upturn, starting with trial 61 when the regular right-left alternation of the positive side of the box was changed to a randomized sequence.

These results demonstrate that *Panulirus* can discriminate the light intensities used in the two compartments and utilize their position as a conditioning stimulus in goal seeking.

2. *Training to polarized light.* In both Series A (inexperienced lobsters) and Series B (experienced lobsters) the error scores were no better than random even at the end of the 6- and 11-day training periods (Fig. 6a, b). The inexperienced animals made a large number of errors (76%) in the first trials, but after 9 trials they made about 50% (Fig. 6a, error curve). Rapid decreases in the proportion

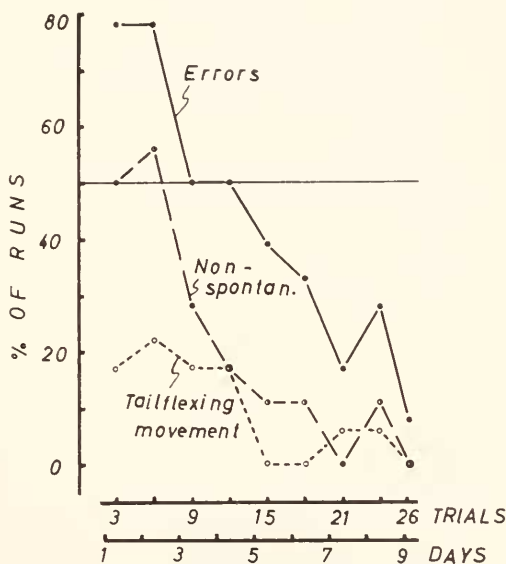


FIGURE 7. Mean learning curves for 6 lobsters training to side. Points indicate percentages of the runs in three trials.

of nonspontaneous runs and runs with tail-flexing movements also occurred in the inexperienced group (Fig. 6a, curve of nonspontaneous and tail-flexing movement runs).

In contrast, with the previously trained animals all three of these scores were about at the same level in the first as in the last trials (Fig. 6b). Although these two series showed that spontaneity and tail-flexing movements reached levels comparable to those attained in the brightness training (Fig. 5), they give no indication that the two tested orientations of the e -vector of polarized light could be used as a conditioning stimulus to discriminate the spatial choice required.

3. *Training to side.* The general behavior of test animals in the above experiments suggested that they readily could learn the side with a reward since they often went toward that compartment which had been the positive one in the previous test.

This was confirmed by the results of experiments carried out to study this type of training. The error score was over 78% at first but decreased precipitously and quite steadily thereafter. It was 50% after 9 trials and about 10% after 26 trials at the end (Fig. 7, error curve). A similar course was run by the proportion of nonspontaneous runs which started at 50% and decreased after 15 trials to 11%. The fraction of runs with tail-flexing movements showed a general trend to decrease from about 20% initially to zero in the last trials.

DISCUSSION

Experience indicates that rate and extent of learning in various animals depend strongly on the particular problem tested and the sensory modalities involved in the afferent components of the process. Also the strength and type of drive and reinforcement involved obviously will markedly affect learning (Hull, 1952). Nevertheless, it seems clear in the present experimental situation that *Panulirus* did not learn even at best to make two-choice spatial discrimination either very quickly or very accurately. Mean error scores for a day never were substantially less than 20% and even these took more than 20 trials to achieve. Thus in the training-to-side experiment the error score dropped markedly below 20% only after 26 trials (Fig. 7) and in the training-to-brightness series an error score markedly below 20% first appeared after 108 trials (Fig. 5).

The differences in learning shown in these two sets of training experiments may reflect the relative importance of different sensory modalities for the type of conditioning involved. The more rapid achievement of < 20% errors in choosing one side than in discriminating between the two circular areas of different brightness suggests that some tactile or kinesthetic cues are more important than visual ones in finding the open exit hole. Such an interpretation is supported by the cases cited above (Fig. 4) where persistent preference for one side was manifest in certain individual *Panulirus* and by previous work on the fiddler crab *Uca* (Schwartz and Safir, 1915) and the crayfish *Pacifastacus* (Gilhousen, 1927) which demonstrated turning predominantly in one direction or following of one wall. Such a preponderant influence of mechanoreceptor afferent information for *Panulirus* is consonant with the animal's normal rocky surroundings in submarine holes and crevices, coupled with its essentially nocturnal habit.

The lack of evidence for the lobsters learning to discriminate between vertically and horizontally polarized light sources is consonant with the conclusion that visual cues are not as significant as certain others in the present spatial choice problem. However, it does not seem to reflect the finding in the crab, *Ocypode*, that vertically polarized light has a significantly greater effect on eyestalk displacement than horizontally polarized light of the same photometric intensity (Schöne and Schöne, 1961).

Previous attempts with other animals to demonstrate discrimination of different planes of polarization by training techniques have yielded both positive and negative results. In the pigeon, food-training discrimination tests gave no evidence for polarized light perception but indicated good light intensity discrimination (Montgomery and Heinemann, 1952), thus resembling some of the present results with *Panulirus*. On the other hand, in the honeybee a significant ability to discriminate vertically from horizontally polarized light was reported on the basis of food-seeking

training (Stockhammer, 1956).⁴ Reward and punishment training in *Octopus* has similarly demonstrated that animal's ability to discriminate vertical from horizontal polarized light as well as between oblique planes of polarization at 45° and 135° to the vertical (Moody and Parriss, 1960, 1961).

However, the present failure to get discrimination learning to polarized light cannot be taken as evidence that the animal does not perceive the plane of polarization, as a great variety of arthropods, including decapod crustaceans, must do (Stockhammer, 1959; von Frisch, Lindauer and Daumer, 1960; Jander and Waterman, 1960; Waterman, Jander and Daumer, unpublished; Schöne, unpublished data). Negative evidence of the sort obtained here merely demonstrates an absence of training effect in the current experimental situation without decisive prejudice to the more general question.

In the learning curves for the error scores of inexperienced lobsters (Figs. 5, 6a, and 7), the occurrence of initial levels significantly above the random choice value of 50% results directly from the way errors were counted. The inclusion of non-spontaneous runs as errors contributed substantially to the initial excess over what would be expected, since inexperienced animals frequently required prodding to initiate and maintain walking.

On the other hand with experienced animals the initial error scores were near 50% (Fig. 6b) and the nonspontaneous runs were much less frequent during the first trials. This raises two points of interest. (1) Retention of training must occur for the period between experiments (3 days). (2) Learning, as evidenced by the reduction in nonspontaneous runs, took place even when the *Panulirus* were not learning to find the open exit. Such data suggest that the test situation consists of at least two stages: (1) learning to walk forward (probably related to the general factor of drive or appetitive behavior (Tinbergen, 1951), and (2) learning to discriminate the positive compartment.

Another point of interest is the correlation of tail-flexing movements with inexperience and with progress in learning. The tail-flexing movements appeared to be characteristic of inexperienced individuals (Figure 2 and the first trials of the appropriate curves of Figures 5 and 7) and of those showing little tendency to learn (Fig. 6). In both of these cases tail-flexing is correlated with error runs. The detailed correlations of tail-flexing movements with correct, incorrect and non-spontaneous runs are shown in Table I which indicates that tail-flexing movements were most prominent in nonspontaneous runs, less so in incorrect runs, and at a minimum in positive runs where the open exit was reached spontaneously.

The protocols show that tail-flexing movements were particularly associated with "indecisive" behavior. Thus, if the lobster (1) was inactive unless prodded with the stick, (2) chose the negative compartment and found the exit blocked, (3) made turns in more than one direction, stopped or walked backwards, then tail-flexing movements were likely to appear suddenly. In cases (1) or (2) above the tail-flexion response could be interpreted as an escape reaction from a threatening situation as it often appears to be for lobsters in the sea when strong external stimulation occurs (such as the nearby appearance of a large fish). However, when the same reaction appeared as a component of "indecisive" behavior patterns lacking

⁴ In these experiments no control is mentioned against the possibility that intensity artifacts due to differential reflection of the polarized light were involved in the training process.

any obvious external threat, the tail-flexing movement would seem to be a displacement activity in the ethological sense (Eibl-Eibesfeldt and Kramer, 1958; Schöne, 1961). Thus, its diminution with experience could be considered as habituation to initially startling or conflicting situations.

SUMMARY

1. Juvenile spiny lobsters (*Panulirus argus*) could be trained in air in a two-choice discrimination box to use two stimulating lights which differed in intensity by a factor of 3-5 times in learning to reach an open exit hole leading to an aquarium containing sea water.

2. Comparable training procedures yielded no better than chance selection of the two compartments (one with the open exit, the other with its exit blocked) when the conditioning lights were of equal intensity but were both linearly polarized, one horizontally, the other vertically. Demonstration that lobsters did not use polarization pattern in this spatial discrimination situation does not prove that the plane of polarization was not perceived by *Panulirus*.

3. Learning was more rapid than it was to intensity differences when the animals were trained always to go to one side of the discrimination box to reach the open exit. For intensity discrimination initial high percentage errors were reduced to less than 20% only on the twentieth day after 104 trials per animal, whereas for training to side less than 20% errors were achieved after 20 trials per animal.

4. Learning indicated by the curve of mean error scores per day resembles an exponential decay function and is accompanied by decreases in percentage of non-spontaneous runs and runs showing tail-flexing movements. Tail-flexing movements were correlated positively with error runs and occurred as a result of "indecisive" behavior.

5. Learning indicated by reduction in percentages of nonspontaneous runs showed retention of training between experiments and continued in cases where exit discrimination was not being learned. Hence over-all training involved: (a) learning to walk directly forward, and (b) learning to discriminate the side with the open exit.

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